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THE DURATION OF MARINE FISH EMBRYONIC DEVELOPMENT AS A FUNCTION OF WATER TEMPERATURE

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[p. 51 of the Russian original]

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THE DURATION OF MARINE FISH EMBRYONIC DEVELOPMENT AS A FUNCTION OF WATER TEMPERATURE

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The physiological processes of cold-blooded animals are known to depend on temperature, and the duration of the incubation period in fish is no exception. Published data on the embryonic development of marine fish [1, 2, 4] makes it possible to examine the nature of quantitative relationships between the duration of the incubation period and temperature (in its interspecies aspect). A knowledge of such relationships is indispensable in dealing with issues involving population productivity and population dynamics.

The purpose of this paper is to find ecologically useful equations that are based on available factual data. Since this paper has not undertaken the task of constructing a detailed model of temperature relationships, an adequate foundation is provided by Beleradek's widely used equation relating the duration of development in cold-blooded animals to temperature. The number of parameters has been reduced for the sake of simplicity ("conditional biological null" has been excluded) and the equation has been given the form:

$$D_0 = aT^{-b}, \qquad (1)$$

where D_0 is the duration of development (in this case, the incubation period) in days, T is the temperature in degrees centigrade, and a and b are constants. For example, the equation has been used in this form to describing the relationship between duration of development and temperature in marine nematodes [6].

The factual data that was borrowed from the aforementioned sources is presented in the table. Whenever the sources gave D_0 and T as limits, the arithmetic mean was taken.

T. V. Dehnik [1] divided Black Sea fishes according to their reproductive method into five groups (Group I: viviparous; II: those bearing their eggs in brood pouches; III: those producing pelagic eggs; IV: those that lay their eggs on a hard substrate; and V: those that nest, , watching over their

offspring). T. S. Rass [5] has proposed a grouping of the floating eggs of marine fish that takes account of 12 morphological features, some of which are undoubtedly reflected in the duration of the incubation period. Consequently, when analyzing temperature relationships, we considered it advisable to examine a large number of groups individually and then to compare them. Improving the classification was not our purpose and so the groups employed are rather arbitrary (for an elaboration of the analysis of the relationship between D_0 and T). The classification of T. V. Dehnik [1] served as a foundation, but the table contains no data on viviparous fish or on those that bear their eggs in brood pouches and so the numeration of the groups has been changed. The group of nesting fish has been split in two (the gobies have been separated from all the others), and the fish with pelagic eggs that was studied by A. Yu. Podosinnikov [4] has tentatively been accepted as an independent group. This makes it possible to compare the quantitative

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relationships that follow from the data of different students of fish with pelagic eggs.

The result of all this was five groups (see the table) for which the values of equation (1) were calculated by the method of least squares, producing the following results:

$$\text{I } \lg D_0 = 2.64 - 1.84 \lg T, \text{ or } D_0 = 436.5\, T^{-1.84} \quad (2)$$

$$\text{II } \lg D_0 = 4.54 - 2.55 \lg T, \text{ or } D_0 = 34670\, T^{-2.55} \quad (3)$$

$$\text{III } \lg D_0 = 2.71 - 1.56 \lg T, \text{ or } D_0 = 512.9\, T^{-1.56} \quad (4)$$

$$\text{IV } \lg D_0 = 3.08 - 1.62 \lg T, \text{ or } D_0 = 1202\, T^{-1.62} \quad (5)$$

$$\text{V } \lg D_0 = 2.39 - 1.7 \lg T, \text{ or } D_0 = 245.5\, T^{-1.7} \quad (6)$$

The Duration of Embryonic Development in Marine Fish

Species	T, °C	D_0, days
	Group I	
Sprattus sprattus	5 - 13	8
Engraulis encrasicholus	20 - 23.4	1.5
Gaidropsarus mediterraneus	13 - 14.5	4
Odontogadus merlangus euxinus	7.2 - 8	8
Mugil cephalus	20	2
M. auratus	21	2
Serranus scriba	22 - 24.6	1
Trachurus mediterraneus ponticus	19.5 - 20.6	1.5
Sciena umbra	20 - 24	1
Diplodus annularis	19.6 - 21	1.3
Mullus barbatus ponticus	22.1 - 23.4	1.4
	17.5 - 18.5	2.1
Ctenolabrus rupestris	19 - 23	1
Trachinus draco	20 - 22	2.7
Uranoscopus scaber	21.4 - 22.9	4.5
Callionymus belenus	21.4 - 25	1
Scomber scombrus	10 - 11	9
	14	5
Sarda sarda	18 - 22	2
Scorpaena porcus	20 - 22	2
Scophthalmus maeoticus	15.6 - 16.6	3.5 - 4
Platichthys flesus luscus	6.8 - 8	7 - 7.5
	Group II	
Atherina mochonpontica	20 - 25	10
A. hepsetus	22	11
Belone belone	23 - 25	12 - 13
	13 - 19	30
	Group III	
Spicara smaris	20.3	5
	21	3.5
Chromis chromis	21.5 - 24	4
Symphodus csina	16.6 - 17	6 - 7.5
	17.5 - 18.2	5
Crenilabrus tinca	10 - 18	5 - 8
C. quinquemaculatus	17.6 - 19	5 - 6
C. ocellatus	20 - 21	4.5 - 5.5

	Group IV	
Pomatoschistus minutus elongatus	18 - 19	9
P. microps leopardinus	20 - 23	10 - 12
Gobius niger	20 - 21	6
G. ophiocephalus	18 - 20	5 - 6
G. bucchichi	21 - 22	5
Neogobius melanostomus	15 - 18	12 - 14
	18 - 22	14
N. fluviatilis	16.7 - 20	21
	18.5 - 25	15 - 17
N. cephalarges	12 - 15	16 - 18
	17 - 18	12 - 13
Mesogobius batrachocephalus	8 - 15	21 - 23
Proterorhinus marmoratus	18 - 21	7
Knipowitschia longicauda	23 - 26	6 - 7
	Group V	
Pomatomus saltatrix	19.9 - 20.6	1.75
Trachurus trachurus	18 - 20	1.7
T. trecae	21 - 26	1.1
Vomer setapinnis	23 - 26	1.1
Umbrina canariensis	21.2 - 24.2	1
Boops boops	23.8 - 26	1.3
Dentex macrophthalmus	19.8 - 21.9	1.3
Pagrus ehrenbergii	23.8 - 26	1.1
Pagellus bogaraveo	17 - 20	1.8
Chaetodon hofleri	22.5 - 26	1
Parapristipoma humile	20 - 25	0.9
P. mediterraneus	19.3 - 26	1.2
Erythrooles monodi	22 - 26.5	1
Trachinus draco	18.3 - 21.3	4.2

Figure 1

The duration of the incubation period in marine fish, D_0, as a function of temperature (in its inter-species aspect). 1a: Fish Group I (1), Group V (2), *Uranoscopus* (3), and *Trachinus* (4); 1b: Group III (1), the data of V. V. Krakatitsa (2), and *Uranoscopus* (3); 1c: gobies (Group IV).

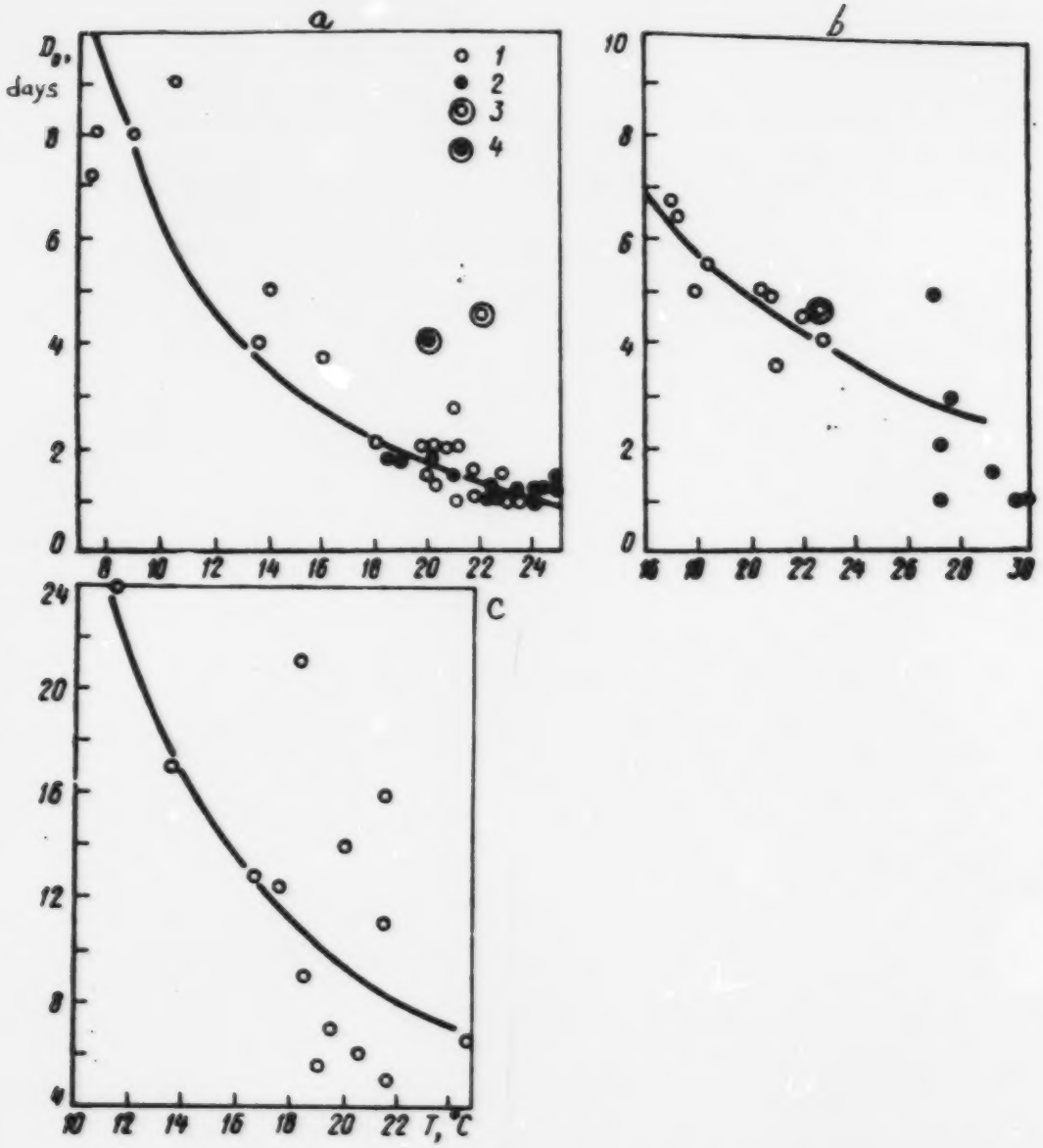
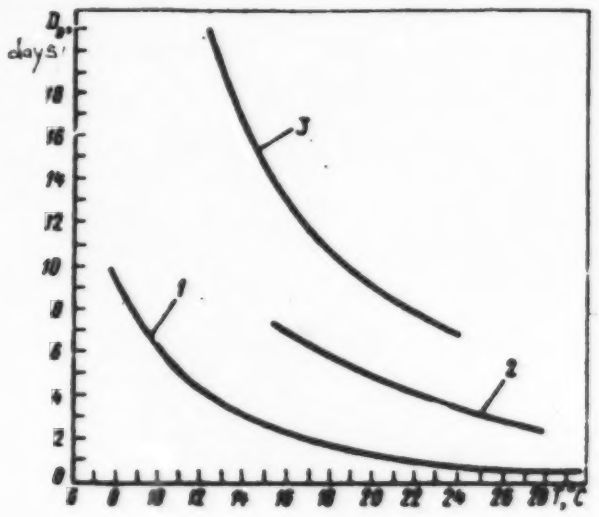


Figure 2
A comparison of the curves of the incubation period of marine fish of different groups as a function of temperature: 1, 2, and 3 correspond to equations (7), (4), and (5), respectively.



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Group I is the best represented (22 points). All of the Black Sea fish included herein have egg sizes of 0.7 – 1.25 mm, with the exception of *Uranoscopus scaber* (2.1 mm). This point stands out from the general range (Fig. 1a) and it was excluded from the calculations. We observe that Group V includes species with an egg size of 0.8 – 1.2 mm, in other words, the same size class as that in Group I. Since equations (2) and (6) are very similar, we can conclude that all these fish species form a single group (this being confirmed by the data of various researchers). Joining Groups I and V, we obtain the following equation

$$\lg D_0 = 2.71 - 1.92 \lg T, \text{ or } D_0 = 512.9\, T^{-1.92} \qquad (7)$$

We should note that according to the data of A. Yu. Podosinnikov [4], *Trachinus draco* clearly does not belong to Group II in terms of the feature being considered (Fig. 1a) and was excluded from the calculations. It should also be observed that, in agreement with the conclusion of T. V. Dehnik, D_0 = 2.7 and not 4 in this species at this same temperature (see the table).

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There are few points in Group II, one of them (*Belone belone* at 16°C) having a very great effect on the magnitude of *b*. We note that in all of the other groups this index does not exceed the limits 1.56 – 1.92. Consequently, equation (3) should not be used. We can only conclude that in those fish with large eggs the duration of embryonic development is greater than the average for gobies at the same temperatures.

Group III is formed by the nesting fish with small eggs (up to 0.85 mm) as opposed to the gobies which include species with both small and large eggs. An analysis of the dependence of D_0 on T has shown that the incubation period in this group lasts longer than it does in Group I. We note that the point considered above for *Uranoscopus* fits well in Group III (Fig. 1b).

Finally, the data on the species studied by V. V. Krakatitsa [3] are similar to that group. This work presents documentation on eggs collected from the sea before incubation, i.e. the exact value of D_0 has not been established. Making use of all this information, we have adopted the following tentative values:

	T	D_0
Sardinella fimbriata	30	1
S. longiceps	30.2	1
Vinciquerria nimbaria	27	1
Muraena sp.	26.8	5
Ophichthus sp.	27.5	3
Fistularia villosa	27	2
Carangoides gallichthys	29	1.5

This data was used to construct a graph (Fig. 1b) that shows the similarity of the species in question to Group III in terms of the relationship between embryonic development and temperature.

Among the gobies (Group IV), the species with small eggs develop in approximately the same way as those of Group III. The species with large eggs display significantly greater values of D_0 at the same temperatures. On the whole, the group of gobies is diverse, which is demonstrated by the scatter of points in the graph (Fig. 1c).

Thus, the analysis that has been made has demonstrated the need to clarify the quantitative relationship of D_0 as a function of T for certain ecological-physiological groups of fish. It seems that the more valid is the division of fishes into groups according to the set of features of embryonic development, the clearer is the quantitative relationship between D_0 and T within each group.

Despite the admitted inadequacy of the division into groups and the need for further refinement, the results that have been obtained allow us to draw some preliminary conclusions that can be used in dealing with ecological problems. Equation (7) may be taken to describe the relationship between D_0 and T in fish with pelagic eggs that are up to 1.2 – 1.3 mm in size. Equation (4) should be used for nesting fish with small eggs, and equation (5) for fish that reproduce in the pelagic zone and have eggs larger than 1.2 – 1.3 mm and

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for the gobies. For the sake of comparison, the curves corresponding to equations (4), (5), and (7) are presented on a single graph (Fig. 2).

According to these equations, when the temperature changes by 10°C, the duration of the incubation period in Group III and Group IV changes by a factor of 2.3 – 2.6, and in the case of Group I by a factor of 3 (4 at low temperatures). This makes it possible to estimate provisionally the deviations in D_0 of similar species for any ocean areas under comparison, and this could be of considerable importance in judging a population's "initial rate of recruitment" (considering the total number of eggs). Let us demonstrate this with a hypothetical numerical example.

Assume investigations to have revealed an identical average population for some species from Group I in two ocean areas (or in the same area at two different seasons). In one case the water temperature was 19°C and in the other, 24°C. According to equation (7) and curve I (Fig. 2), in the first case D_0 = 2 days and in the second, D_0 = 1 day. This means that the total number of eggs recorded in the first is produced by two days of spawning, and in the other case in only one day (since the ovular stage is completed at the end of the period D_0). To put it another way, when the total number of eggs is uniform and the temperature difference is 5°, in the first case the rate of appearance of eggs in the sea because of reproduction is only half as much. The ecological importance of such differences is obvious.

This illustrates the importance of the temperature relationships that have been revealed in solving ecological problems.

In conclusion, the authors feel it their obligation to express their gratitude to A. D. Gordina for useful advice during the course of their work.

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